Age structure and survival rate in Alpine newts (*Triturus alpestris*) at high altitude

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Individual ages of 67 Alpine newts from a karst plateau in the Northeastern Calcareous Alps of Austria (Totes Gebirge, 1650 m altitude) have been assessed using skeletochronology of cross sections of the humerus. Both sexes start to reproduce at the age of 10 years, longevity exceeds 20 years and the oldest animal survived to an age of 22 years.

Survival rates estimated from age structure and mark-recapture experiments appeared lower in males, causing a female-biased sex ratio. Males may be subject to increased mortality during the spring migration.

INTRODUCTION

Skeletochronological studies of *Triturus* have shown that age at first reproduction is delayed and longevity increased with increasing altitude and latitude of the breeding site (DOLMEN, 1983; CAETANO et al., 1985; CAETANO, 1990; CAETANO & CASTANET, 1993). Decreased ambient temperatures lead to reduced metabolic rates, which in turn cause slower growth and delayed sexual maturity (JØRGENSEN, 1992). Age and survival in the Alpine newt were studied on the southwest plateau of the Totes Gebirge (1650 m), the largest karst massif (590 km^2) in the Northeastern Calcareous Alps of Austria. This massif generally receives more than 2200 mm precipitation annually and snow cover is present more than 196 days each year (DINÇER et al., 1972), breeding sites were covered with ice from the beginning of November until mid-June during the study period. Some of the breeding sites are former dolines, where temperatures are reduced by the settling of cold air.

MATERIAL AND METHODS

Alpine newts were collected from Lake Dreibrüdersee (1643 m) and from a pond (1650 m) situated approximately 1 km east from the lake in a neighbouring valley. A mountain range with peaks up to 1950 m separates the two breeding sites. Lake

Dreibrüdersee fills a former doline (137 m diameter) and is surrounded by steep rocky slopes.

Individual ages of 36 females and 8 males from Lake Dreibrüdersee, and 23 males from the nearby pond, were assessed by skeletochronology using cross sections of the humerus. Mean snout-vent lengths of breeding females and males in Lake Dreibrüdersee were 57.06 ± 0.22 mm (95 % C.L.) and 49.53 ± 0.32 mm respectively. Only males found dead were used for age determination. Live females were anaesthetized with MS 222 and the entire sample was fixed in 10 % formalin. Diaphysial regions of the humerus were decalcified with 40 % EDTA, dehydrated in Isopropylalcohol, stored over night in Methylbenzoat, and embedded in Paraplast. Cross sections 10 mm in thickness were stained with DELAFIELD-Hematoxylin (ROMEIS, 1968) for several hours and then destained with hydrochloric acid.

The mean survival rate (Φ) for the age classes 14 to 19+ in females from Lake Dreibrüdersee and 14 to 17 in males from the pond were calculated from the age structure by using the ROBSON & CHAPMAN formula (KREBS, 1989: 432-433):

$$\Phi = \frac{T}{\Sigma N + T - 1}$$

where:
Φ = average finite annual survival rate or probability of survival; finite survival rates can range from 0 to 1; a survival rate of 0.65 means that in average 65 % of the population survive from one year to the next;
N_x = number of individuals in age class x;
ΣN = number of all animals from age classes x to x+i: $N_x + N_{x+1} + N_{x+2} + \ldots + N_{x+i}$; for females from Lake Dreibrüdersee this is: $N_{14} + N_{15} + \ldots + N_{19+}$;
T = sum of the coded ages times their frequencies when coded age is found by setting the youngest included age class to 0, the next age to one and so forth: $0N_x + 1N_{x+1} + 2N_{x+2} + \ldots + iN_{x+i}$, for females from Lake Dreibrüdersee this is: $N_{15} + 2N_{16} + \ldots + 5N_{19+}$.

Animals from age classes 10 to 13 were omitted from the calculations because they were underrepresented in the sample (fig. 2).

This formula is only valid for a stationary population in which recruitment and survival are relatively constant. As these assumptions are hardly fulfilled in natural populations, the calculated values should be treated as rough estimates which allow comparison of average survival rates between sexes and between different populations.

Adults (855 females, 277 males) in Lake Dreibrüdersee were marked individually by tattooing with Alcian blue between 1986 and 1992 (JOLY & MIAUD, 1990) Population size and finite annual survival rates were estimated with a multiple mark-recapture census (JOLLY-SEBER method, KREBS, 1989: 37-43). In contrast to the ROBSON & CHAPMAN method this model does not assume a constant survival rate.

Reliability of population size estimates was assessed using less complex models (PETERSEN and SCHUHMACHER methods, KREBS, 1989: 16-36) which work only in a closed

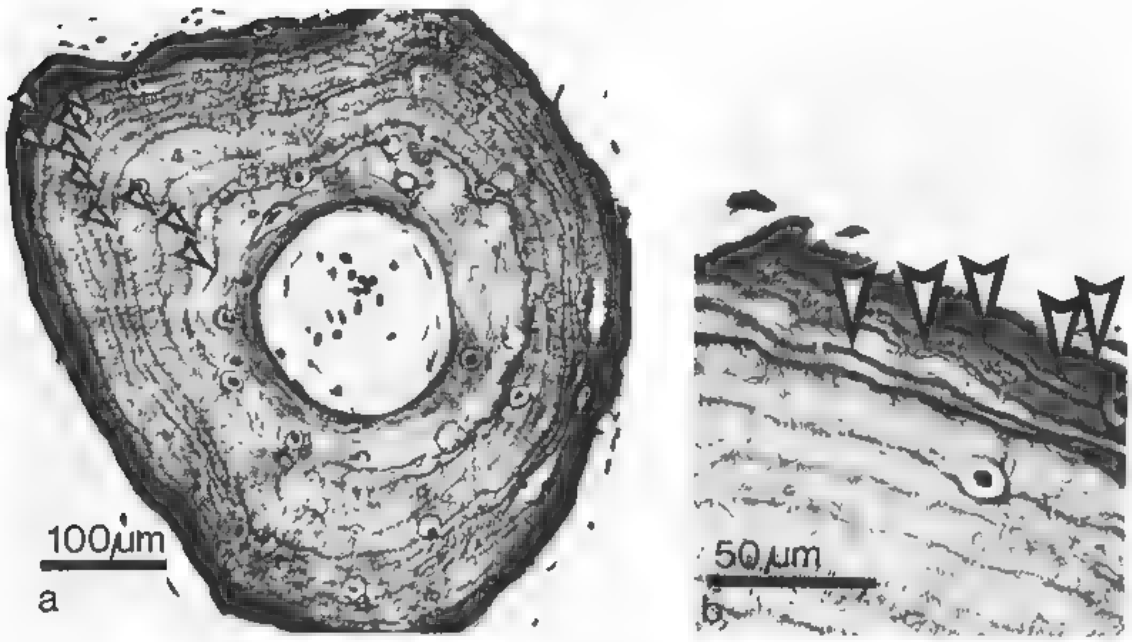

Fig. 1 – Cross section of the humerus of a 15 years old Alpine newt female. a: LAG formed during the first 10 years of life. b. LAG become narrow after the newt starts to reproduce Fig. 1b is taken from another cross section of the same bone shown in fig. 1a

population. During the summer period the percentage of marked animals in consecutive samples increased linearly with the total amount of newts marked in this year (SCHUHMACHER-ESCHMEYER plot; KREBS, 1989 35), showing that a constant population size was reached for a short time interval after migration into the lake.

RESULTS

No marked animals from Lake Dreibrüdersee were found in other breeding sites. Due to the isolated position of the lake and the high recapture rates of individually marked newts, any interchange with other populations seemed unlikely. There was no other breeding pond available in the vicinity of Lake Dreibrüdersee.

Both sexes started to breed late in life, first entering the breeding site at the age of 10 years. The long winter period resulted in clear lines of arrested bone growth (LAG), which were very close together after the animals had started to reproduce (fig. 1a). After 10 years age, bone growth was strongly reduced, resulting in a darkly staining outer zone of narrow LAG (fig. 1b). No animals younger than 10 years age were caught in the breeding sites indicating that the younger newts in this population lead an entirely terrestrial life.

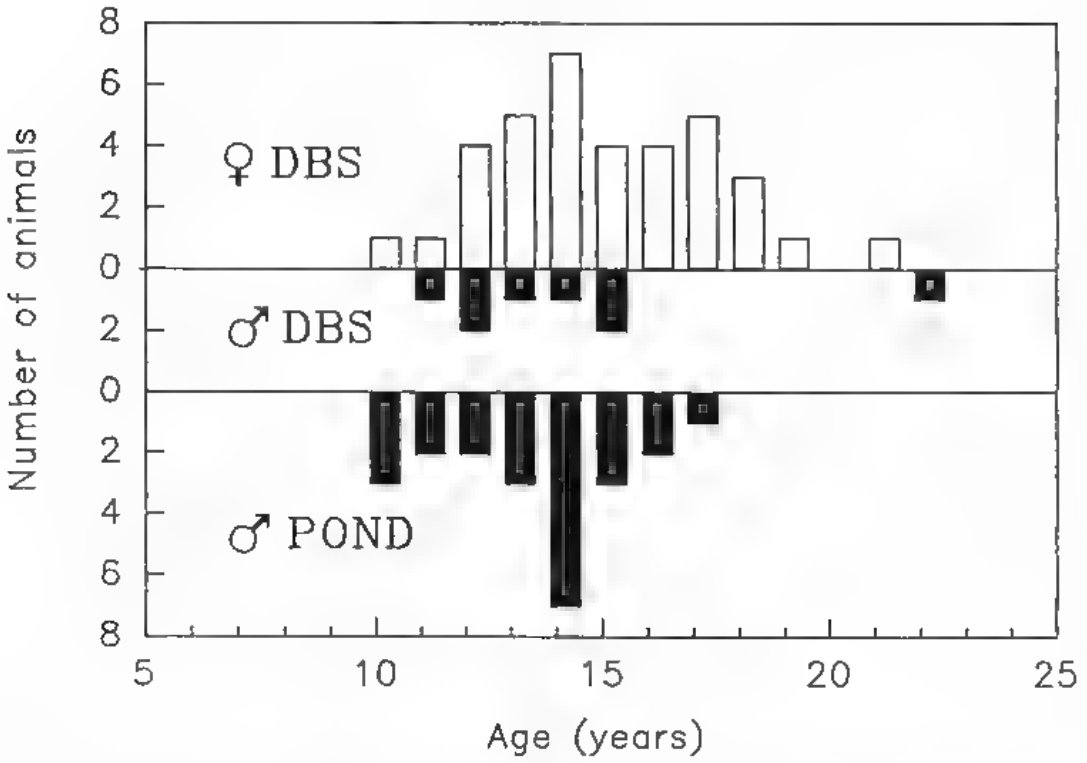

Fig 2. – Age structure of the breeding populations of Alpine newts from Lake Dreibrüdersee (DBS) and a nearby pond.

Animals 14 years old constituted the largest age class (fig. 2). Longevity exceeded 20 years in one female and one male newt from Lake Dreibrüdersee. The average annual survival rate derived from the age structure was estimated to be 0.67 ± 0.003 ($\Phi \pm$ S.E.) for females from Lake Dreibrüdersee and 0.45 ± 0.012 for males from the pond, meaning that on average 67 % of the females and 45 % of the males survived from one year to the next.

Estimates of annual female survival rates (JOLLY-SEBER method) were above 0.70 (Table I) Approximately 60 % of the females ($\Phi \pm$ S.E. = 0.609 ± 0.043) and 40 % of the males (Φ = 0.397 ± 0.087) present in 1986 survived to 1988. Assuming a constant probability of survival in this two-year interval yields annual survival rates of 0.78 and 0.63 for females and males, respectively. From 1988 to 1992, the sample size of males was too small for application of the JOLLY-SEBER model. The results indicate that males suffered from higher mortality than females.

The newt population in Lake Dreibrüdersee consisted of approximately 500-800 females and 150 males, resulting in a biased sex ratio of 1/3.7 to 1/4.8 males to females (Table I). Estimates of population size with different mark-recapture models were within the confidence limits of each other.

Table I. - Population size, sex ratio and survival rate of Alpine newt adults in Lake Dreibrüdersee estimated with mark-recapture experiments. Sex ratio: ♂/♀. No animals were marked in 1987.

Year	Population size (N)		Survival rate $\Phi \pm$ S.E.
	PETERSEN [P] / SCHUHMACHER [S] (95 % C.L.)	JOLLY-SEBER N ± S.E.	
1986	♀: 773 (541-1314) [P]		1986-1988: ♀: 0 609 ± 0.043 ♂: 0.397 ± 0 087
1988	♀: 517 (466-580) [S] ♂: 149 (125-184) [S] Sex ratio: 1/3.5	546 ± 40	0.824 ± 0.053
1989	♀: 708 (609-845) [S] ♂: 156 (122-232) [P] Sex ratio: 1/4.6	807 ± 58	0.747 ± 0.090
1990	-	664 ± 86	0.965 ± 0.186
1991	♀: 682 (321-1443) [P]	596 ± 102	-

DISCUSSION

Alpine newts in temperate environments start to reproduce at three to four years of age and live for a maximum of 10 years (SMIRINA & ROČEK, 1976, SMIRINA & SUFIANIDU, 1985; MIAUD, 1990). The present study has shown that first reproduction can be significantly delayed due to cold temperature conditions. Adults have to use a very short summer period for reproduction. The average yearly ambient temperature at Lake Dreibrüdersee is around 2° C, resulting in slow growth rates. Growth is further reduced with the onset of first reproduction, as more energy has to be put into gonadal development. Strongly reduced bone growth after 10 years age and the fact that no younger animals were caught in the breeding sites indicate that Alpine newts cannot reproduce earlier in life under these environmental conditions

Animals from Lake Dreibrüdersee were bred under laboratory conditions simulating lowland temperature regimes. They reached body size of breeding animals within two to three years, showing that reduced growth was not genetically determined in this population (pers obs) Food availability was high in Lake Dreibrüdersee and reduced growth did not result from limited resources in the lake. During the second half of their aquatic period, individually marked females regained biomass lost during oviposition (pers. obs.).

A long phase of hibernation followed by a comparatively short period of activity in summer probably did not support the development of double LAG reported for other *Triturus* populations (CAETANO et al., 1985; CAETANO & CASTANET, 1993).

The average female survival rate calculated with the ROBSON & CHAPMAN formula is close to the estimate of 0.65 published by MIAUD (1991) for a lowland Alpine newt population in south-east France. Nevertheless, mark-recapture experiments yielded higher survival rates above 0.7 (Table I). This difference resulted from not including age classes 10 to 13 in the calculation of survival rate with the ROBSON & CHAPMAN formula. Some of the 10 to 13 years old specimens did not enter the breeding sites. Additionally, the age of animals older than 15 years may have been underestimated, because LAG became increasingly more difficult to distinguish. For this reason mark-recapture experiments gave a more realistic description of survival.

Males seemed to have a higher mortality rate than females. These different survival rates in males and females clearly need to be investigated further. In their detailed studies of Alpine newts at similar altitudes in the Austrian Alps, FABER (1991) and GUTLEB (1990) also found skewed sex ratios of 1/1 45 and 1/1 22 males to females respectively. Higher mortality during the spring migration could be the reason for the lower survival rates in adult males. Adult males started spring migration before the females. This was also found for other newt species (BLAB, 1978; HARRISON et al., 1983; GRIFFITHS, 1984). During migration at the beginning of June, temperature often drops below freezing At this time males enter numerous small water bodies on their way to the breeding site. These puddles easily freeze and the newts suffocate. Of 50 dead newts collected in the spring 48 were males.

RÉSUMÉ

L'âge individuel de 67 Tritons alpestres d'un plateau karstique des Alpes calcaires du nord-est de l'Autriche (Totes Gebirge, altitude 1650 m) a été mis en évidence par squelettochronologie s'appuyant sur des coupes transversales d'humérus. En raison de la longue période d'hiver, les animaux des deux sexes commencent à se reproduire à l'âge de 10 ans L'espérance de vie s'élève à 20 ans, l'animal le plus vieux observé ayant atteint l'âge de 22 ans Le taux de survie, estimé en fonction de la structure d'âge de la population et d'expériences de marquage-recapture, semble plus bas chez les mâles, ce qui entraîne un biais du sex-ratio en faveur des femelles Ce phénomène pourrait être dû à une mortalité élevée des mâles pendant la migration de printemps.

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